

THE LIFE HISTORY OF
PHALACROGNATHUS MUELLERI (MACLEAY)
(COLEOPTERA: LUCANIDAE)

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Abstract

The life history of *Phalacrognathus muelleri* (Macleay) is described and aspects of its biology discussed. The species is restricted to the wet tropics of northern Queensland where it breeds in rotting wood in rainforest. Larvae have been extracted from the wood of 27 tree species in 13 families. All larvae found were in wood attacked by white rot fungi. The final instar larva is described. Larva, pupa, and parasites are figured.

Introduction

Phalacrognathus muelleri (Macleay) (Coleoptera: Lucanidae) is a well known but poorly documented species. It is variously known as the golden, rainbow, magnificent, Mueller's and king stag beetle, and is the largest Australian member of its family. It is illustrated as the centrepiece to colour plates in both the major textbooks on Australian insects, viz. Tillyard, 1926 and CSIRO, 1970. Since 1973 it has been the official symbol of the Entomological Society of Queensland. The history of the discovery of *P. muelleri* is an interesting story and we have included it here in some detail. The authors wish to thank Dr Geoff Monteith (Queensland Museum, Brisbane) for providing the information in the following two paragraphs.

P. muelleri was initially described as a new species of *Lamprima* in 1885 by Sir William Macleay in Sydney on the basis of a single female from "North Australia" sent to him from Victoria by Charles French Snr (Macleay, 1885a). French was later Government Entomologist in Victoria but at that time he was assistant to the redoubtable Victorian Colonial Botanist, Baron Ferdinand von Mueller. Macleay noted that French had asked him to name the beetle after von Mueller, a request ". . . to which it gives me great pleasure to comply . . .". Macleay speculated that the species "may well form the type of a new genus . . . but in the absence of a male specimen . . . it would be premature . . .". This prompted French, perhaps with a twinge of conscience, to immediately send Macleay the male specimen he had held back previously, and in the same year Macleay published a second paper (Macleay 1885b) erecting the new genus *Phalacrognathus*. Macleay described the male as "I think the most beautiful insect I have ever seen, not surpassed in brilliancy of metallic lustre by the most gorgeous of the Buprestidae".

Macleay exhibited the female specimen at the Linnean Society meeting in Sydney on 29 April 1885 where it "excited much attention" (Anon. 1885a) and he exhibited the male at the same venue on 30 September (Anon. 1885b). The origin of those specimens which French sent Macleay remains a

mystery. At that general time von Mueller was employing botanical collectors to work in north Queensland. One of these was William Sayer, who was also a cousin of Charles French. Another collector in north Queensland at that period was Walter Froggatt who, according to Musgrave (1932), sent insect specimens to both French and von Mueller. It is very likely that French's *Phalacrognathus* came from either Sayer or Froggatt. Contemporary entomologists were also curious about the origin of those exciting specimens. At the meeting of the Linnean Society of New South Wales in 1892 Mr A.S. Olliff enquired". . . as to the exact habitat of the splendid lucanid beetle . . . described by Sir William Macleay . . . about which the only information then available was that they came from North Australia?" Mr F.A. Skuse, then entomologist at the Australian Museum, replied that specimens had recently been received by the Museum from "Russell Scrub, Boar Pocket, near Cairns, Queensland" (Anon. 1892). This locality was a popular staging post at that time on the newly opened pack trail from Cairns to the Herberton tinfields via the Mulgrave River and presumably this is how the collector of those specimens would have accessed the area. Much is now submerged under the Tinaroo Dam at the north end of the Atherton Tableland (Toohey, 1994). The species was redescribed under the synonymic name of *Phalacrognathus westwoodi* by Shipp (1893) from a single male in the Oxford University Museum. This specimen had been purchased by Professor Westwood from the dealer Boucard in 1889 and came from the same uninformative locality as had French's specimens: "North Australia".

The few papers published on the biology of this species are largely the result of casual observation (Brooks 1970, Hancock 1970, Dodd 1971, Brunet 1981, Quick 1984). This paper provides detailed information on the biology and natural history of this the most beautiful of Australian beetles. Observations were made over a period of 14 years on a large number of specimens of all stages, taken in the wild or bred in captivity.

Distribution and Abundance

Phalacrognathus muelleri is confined to the rainforests and adjacent wet sclerophyll forests of coastal north-eastern Queensland between Helenvale (15°43'S 145°14'E) near Cooktown and Pine Creek (19°15'S 146°28'E) at the southern end of the Paluma Range. It is referred to variously as very rare (Britton 1970) or extremely rare (Hawkeswood 1987). As pointed out by Wood and Hasenpusch (1990), this conclusion is likely a result of the species only occasionally coming to light, the most frequently used method of insect survey and collection in rainforests. Our study found *P. muelleri* to be common in virtually any rainforest block within its known distribution, although seemingly more abundant on the ranges and tablelands than at sea level. As the total area of rainforest within its distribution is an estimated



Figs 1-8. Third instar larva of *Phalacrognathus muelleri*. (1). Head capsule (mandibles removed); (2). epipharynx, ventral view; (3). left mandible, dorsal view; (4). antenna, inner surface; (5).apex of hind leg; (6). pars stridens on mesocoxa; (7).plectrum on metatrochanter; (8). raster on ventral side of abdominal sternite 10 . (Scale lines = 1 mm).

7910 km² (Bell *et al* 1987), *P. muelleri* can certainly not be described as rare.

Breeding Sites

Phalacrognathus muelleri breeds in rotting wood in both fallen and standing living or dead trees. Larvae may be found in suitable decayed wood with a minimum volume of approximately 10 litres (0.01 cubic metres). Although *P. muelleri* larvae prefer moderately moist conditions they have also been found in both dry and saturated substrates; waste wood left by logging operations is commonly used. Waste wood tends to be available for a relatively short time when compared to unlogged forests where food supply is continuous. In standing trees where there is an abundance of substrate, such as dead portions of a large, living tree, some individuals may complete their life-cycle without leaving the confines of the trunk. Adults feed on the same material as the larvae and supplement their diet with plant sap and fruits. Trees up to 1.5 m in diameter and containing up to 35 cubic metres of wood have been found as suitable. An indicator of this may be a fallen branch riddled with larvae. Such trees can support generations of beetles.

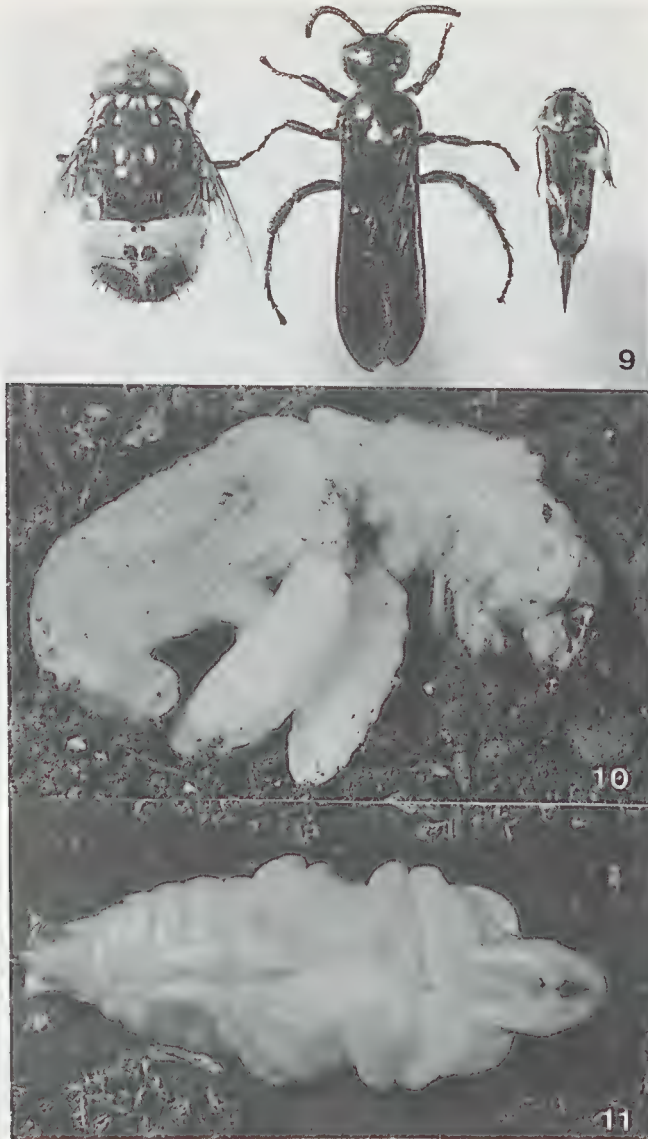
Life History

Oviposition and Egg

Up to 50 eggs are laid by each female, either in wood pulp produced by the female as she excavates a tunnel with her mandibles and tibial spines or in pulp produced by older larvae. Substrate the consistency of balsa is suitable for oviposition. Although each egg is deposited singly, females have been observed to lay up to 30 eggs in close proximity. Captive females laid readily in whole pieces of substrate of suitable size but did not oviposit in artificially produced pulp from the same timber. Newly laid eggs are 2.9-3.7 mm long and 2.2-2.8 mm wide. The surface is smooth with distinct, fine, hexagonal microsculpture, and they are slightly longitudinally flattened in shape. Eggs take 10-14 days to hatch, each expanding to become almost spherical and approximately doubling in volume as they mature. Colour changes from translucent white to dark cream. The larva is visible within the egg just before emergence. The egg splits lengthwise on hatching but a seam or ridge is not visible beforehand.

Larval Description and Behaviour

Of the 18 genera of Lucanidae currently recognised in the Australian fauna (Moore and Cassis 1992), the larval stage has been described for very few. Alderson (1975a, 1975b) compared and partially described species of *Lamprima* Latreille, *Lissapterus* Deyrolle, *Lissotes* Westwood, *Syndesus* W.S. Macleay and *Ceratognathus* Westwood. Lawrence (1981) discussed larval Lucanidae in general and although he examined larvae of ten Australian genera (including *Phalacrognathus*), he did not include formal descriptions but did provide a partial larval key to genera and higher



Figs 9-11. (9). Parasites and ? hyperparasite of *P. muelleri* larvae (from left to right): *Amphibolia ignorata* Paramonov (Tachinidae); *Liacos insularis* (Smith) (Scoliidae); *Mordella elongatula* (Macleay) (Mordellidae); (10). Larva of *Liacos insularis* (Smith) attached to final instar *P. muelleri* larva; (11). Pupa of male *P. muelleri* showing lateral spines on apical abdominal segment.

categories. It is beyond the scope of this paper to discuss the larval relationships of *P. muelleri*. However, the following description of the final instar larva and illustrations of some characters used in the classification of lucanid larvae are provided:

Head (Fig. 1). Maximum width 7.2 - 12.0 mm. Colour light brown with posterior 2/3 of clypeus, antennae and labrum darker brown, anterior frontal angles and mandibles black. Frontal setae (pairs): 1 anterior angle, 1 anterior, 1 exterior, 2 posterior. Clypeus slightly convex with lateral seta and a short lateral tubercule. Labrum obtusely pointed apically. Left mandible (Fig. 3) with 3 apical teeth, right mandible with two, both mandibles with a shallow groove on outer side from base for about half the length. On the epipharynx (Fig. 2), haptomerum with 5 sensilla in a straight line, chaetoparia with 6-11 scattered setae towards outer margin, phobia semicircular, irregular, mostly made up of short blunt spines, epitorma narrow, about 1/3 length of phobia, pternotormae short, obtuse, two well sclerotized lateral and one medial nesia in the haplolachus. Oncylus of hypopharynx strong, triangular, apex acute. Antennae (Fig. 4) 4-segmented, first segment short almost completely fused to the second long, glabrous segment, third segment shorter with inner, irregular lateral and oval, subapical sensory patches, fourth segment short with two setae midway along inner margin, and one seta on subacute apex.

Thorax. With a pair of dorsolateral sclerotized plates just behind head and a pair of ventral sclerotized plates in front of procoxa, meso- and metapleural lobes sclerotized above legs. Tibiotarsus, femur, and trochanter of each leg with ventral and lateral surfaces strongly granulate at base of each seta. Tarsungulus (Fig. 5) short, blunt, with an apical and a subapical seta. Pars stridens (Fig. 6) an area of confused microgranules, with a row of about 50-60 distinct larger granules along outer edge, increasing in size towards apical end. Plectrum (Fig. 7) consists of confused granules at apical end, grading to a single series of about 30 granular rows finally becoming oval, striated plates nearest coxa.

Spiracles C-shaped, thoracic largest, abdominal spiracles 4 and 5 smallest.

Abdomen. Dorsal surface of all abdominal segments with fields of short to long posteriorly directed setae, setae longest near the posterior margin of each segment. Raster (Fig. 8) present on ventral surface of segment 10 in the form of a V-shaped band of spinules, interrupted at apex. Upper anal lobe transverse, triangular, bare, crescent shaped on outside of lateral anal lobes.

Larvae live singly, but often in close proximity, within the decaying wood and may travel several metres through it as they develop. Excavated pulp is packed behind as the larva moves forward. Pieces of substrate are isolated by the mandibles and then grasped by the mandibles and legs and passed backwards. This action is achieved by arching the body upwards in the

Table 1. Host Tree Species for *P. muelleri* larvae

Family	Species	No. of Samples
Apocynaceae	<i>Alstonia scholaris</i> (L.) R. Br.	*
Cunoniaceae	<i>Ceratopetalum succirubrum</i> C.T. White	12
Cunoniaceae	<i>Caldcluvia australiensis</i> (Schltr.) Hoogl	7
Elaeocarpaceae	<i>Sloanea australiensis</i> (Beth.) F. Muell.	2
Elaeocarpaceae	<i>Sloanea</i> sp.	2
Flindersiaceae	<i>Flindersia pimenteliana</i> F. Muell.	3
Flindersiaceae	<i>Flindersia pubescens</i> F.M. Bail.	1
Lauraceae	<i>Beilschmiedia bancroftii</i> (F.M. Bail.) C.T. White	4
Lauraceae	<i>Beilschmiedia</i> spp.	3
Lauraceae	<i>Cryptocarya mackinnoniana</i> F. Muell.	1
Lauraceae	<i>Endiandra monothyra</i> B. Hyland <i>ssp. monothyra</i>	1
Meliaceae	<i>Dysoxylum</i> sp.	1
Meliaceae	<i>Synoum muelleri</i> C. DC.	*
Mimosaceae	<i>Acacia melanoxylon</i> R. Br.	1
Monimiaceae	<i>Daphnandra repandula</i> F. Muell.	1
Monimiaceae	<i>Doryphora aromatica</i> (F.M. Bail.) L.S. Smith	1
Moraceae	<i>Ficus</i> - 2 spp.	*
Moraceae	<i>Ficus</i> sp.	1
Myrtaceae	<i>Eucalyptus torelliana</i> F. Muell.	*
Myrtaceae	<i>Xanthostemon whitei</i> Gugerli	1
Proteaceae	<i>Cardwellia sublimis</i> F. Muell.	5
Proteaceae	3 Proteaceae spp.	3
Rutaceae	<i>Halfordia kendack</i> (Montr.) Guill.	1
Sapotaceae	<i>Palaquium (Lucuma) galactoxyla</i> (F. Muell.) H.J. Lam	*

* Hancock (1970.)

Table 2. Fungi associated with *P. muelleri* larval development

Family	Species	No. of Samples
Ganodermataceae	<i>Ganoderma applanatum</i> (Pers.) Patouillard	4
Polyporaceae	<i>Nigrofomes melanoporus</i> (Mont.) Murr.	1
Polyporaceae	<i>Phellinus</i> nr. <i>glaucescens</i> (Petch) Ryvarden.	10
Polyporaceae	<i>Phellinus robustus</i> (P.Karst) Baird. & Galz.	1
Polyporaceae	<i>Phellinus</i> - 3 spp.	24
Polyporaceae	<i>Pycnoporus</i> sp.	2

centre, which draws the head under the body. Further movement is achieved by peristaltic movement in the folds of the surface of the thoracic segments. As the larva straightens, material is pressed into the rear wall of the cell. These arching and pressing movements are also used in the production of

oval ecdysal cells before moults. These cells are lined with faeces. Arching into a "C" shape the larva deposits a faecal pellet between the legs. The pellet is broken up with the aid of the mandibles and the larva then uses the flat anterior surface of the head to compress the faecal material on to the cell wall. Each ecdysal cell takes about 24 hours to construct. A few hours after completing the cell the larva moults, eating the cast skin before breaking out of the cell several hours later.

Each larva passes through three instars. From egg to adult takes a minimum of 12 months, with the larval stage a minimum of 11 months. Hancock (1970) reported the pupal stage lasting 4-5 weeks and observed length of time in this study was 3-5 weeks. Larvae that develop in 12 months produce small adults. Larger specimens take 2 to 3 years to develop. Specimens in poor quality substrate may take 4 years to develop and are usually small.

Larval Host Plants

Like most members of the family Lucanidae, larvae of *P. muelleri* feed on decaying wood of various species of trees. Authors names of tree species mentioned here are given in Table 1. Two of the earliest records (Hancock 1970, Britton, 1970) of a suitable species were red cedar (*Toona australis*). Monteith (pers. comm.) felt that both these records were based on the opinion of the late George Brooks, an avid beetle collector based many years in Cairns, that a 'red-timbered log' from which he had taken *P. muelleri* specimens on several occasions was this species. Brooks (1970), about the same time, however, obtained an identification for the log in question which turned out to be *Synoum muelleri* C.DC. (Meliaceae). The record of *Synoum muelleri* cited by Brooks (1970), repeated by Hancock (1970), was later suggested to be a misidentification (J.G. Brooks, pers. comm. to D.L. Hancock) and requires confirmation. Other host records cited by Hancock (1970), apart from *Toona australis*, were supplied by R. Parrott (D.L. Hancock, pers. comm). *Toona* did not produce any specimens of *P. muelleri* in the current study, so should be removed from the host list. Hancock (1970) recorded four other species as hosts, namely *Palaquium* (as *Lucuma galactoxyla*), *Cerbera manghas*, and *Ficus* spp. (two species). It is likely that *Cerbera manghas* (Milky Pine) is in reality *Alstonia scholaris* as the former is primarily a sea level species, the latter being found on the Atherton Tablelands proper (Monteith, pers. comm.). Table 1 gives the tree species recorded in this study. The records of Hancock (1970) are also included except for the removal of *Toona* and the substitution of *Alstonia* for *Cerbera*. A large percentage of logs containing *P. muelleri* larvae have decayed to a point where species identification is not possible. Undoubtedly other tree species are also suitable. Timber samples from logs infested by *P. muelleri* larvae were identified by officers of the Queensland Forest Service. Leaf specimens from living trees were identified by Bernie Hyland of CSIRO, Atherton (5 species).

Host trees need to be infected with fungi to be suitable for *P. muelleri* larvae. It would appear that the tree species is less important than that suitable white rot must be present in the wood. In general, white rot is indicated by a pale discolouration of the wood, a result of the darker coloured lignin being removed. Colour ranges from white to pale brown and may include dark zone lines and "pockets". White rot tends to have a "stringy" texture. White rot chemistry is not uniform and we found that not all white rot wood is suitable substrate for *P. muelleri*. Fungal determinations are also rendered progressively more difficult as the substrate deteriorates. Table 2 gives fungal species recorded in this study as associated with *P. muelleri*.

Pupation

The pupal cell is constructed in a similar manner to the other ecdysal cells but takes up to a week to complete. In addition to the lining of faecal matter the cell walls are coated with an amber fluid. The anal segment of the abdomen is used as a "brush" in this process. The source and purpose of this coating is unknown.

The pupa has previously been illustrated. Hancock (1970) gives a line drawing and Brunet (1983) gives colour photographs of a pupa and newly emerged adult.

Hancock (1970) reported moult to pupa occurring approximately two weeks after completion of the pupal cell. The pupa can rotate in the pupal cell on its longitudinal axis using of a pair of lateral spines on the apical abdominal segment (Fig. 11). These spines grip the cell wall and the pupa rotates as it arches and twists sideways. The pupa changes position in the cell many times during development. As the legs begin to harden prior to adult emergence, the pupa rolls on to its back. When the legs become rigid the pupal skin around them is transparent. After then rolling back on to its legs the pupal skin is shed. This commences with the pupal skin splitting down the middle of the dorsal surface of the pronotum. The adult may remain within the pupal cell for up to 8 months before emergence.

Adult Morphology and Behaviour

Males vary in length (measured from tips of mandibles to elytral apex) from 24-72 mm and females from 23-46 mm. As an expression of percentage of total length, male mandibles vary between 19 -32%, irrespective of beetle size. Two males have been recorded with asymmetric mandibles. No variation in mandibular development is apparent in females. A small percentage of non-teneral adults display a shift in colour to either increased red or green. Very rarely is either colour absent but several dark blue specimens have been recorded. Dodd (1971) also recorded rare examples that were very dark in colour.

In breeding large numbers of specimens of this species in this study, females were found to outnumber males by approximately 4%. Dodd (1971), however, stated that in the field males greatly outnumber females.

Adults break out of their pupal cells using the mandibles and legs. Males with well developed mandibles use the base of these for chewing, raking excavated material out with the tarsi. Upon emergence from the pupal cells adults disperse in search of food, mates and oviposition sites. Adults are known to live for up to 18 months in captivity. Light trapping records indicate peak activity at and just after dusk from September to April.

Adult feeding has been observed on *Eucalyptus* sp. blossom, on the fruit of *Calamus moti* Bailey (Arecaceae) (M. Walford-Huggins pers. comm.) and on sap flows associated with insect damage (E. Adams pers. comm.). Dodd (1971) noted that adults were taken on *Glochidion ferdinandi* (J. Muell.) F.M. Bail. (Euphorbiaceae) where hepialid or other wood borers had left a sap-exuding injury. Another apparently less favoured food plant is *Caesalpinia* sp. (Caesalpiniceae), a robust thorny leguminous creeper; in this case the beetle occurring on terminal shoots (Dodd 1971). All records except the first involved feeding during the day.

Oviposition occurs throughout the year in captivity and in the wild. Males have been recorded in the company of ovipositing females and mating has been observed on numerous occasions in captivity. Mating, together with conflict between males, also has been observed at feeding aggregations in captivity.

Adults being handled rarely fold in their legs and remain rigid; they usually claw with the tarsi and may attempt to bite. Males may adopt a threatening stance by rising up on the mid and hind pairs of legs, with forelegs outstretched and mandibles working like scissors.

Males use their mandibles as levers when in conflict with one another. Two protagonists approach each other with the mandibles lowered. Each beetle tries to pass beneath its opponent's body or legs, at which point the mandibles are raised in an attempt to dislodge the rival. On vertical surfaces combatants may be thrown into the air. On horizontal surfaces one may be rolled over and in the grappling that ensues tarsi are sometimes bitten off.

Males also have been observed using their mandibles to facilitate mating. If the female is in a position where she cannot be successfully approached, the male may use his mandibles to lever her into a better position. Where escape or concealment is attempted the male may use his mandibles to violently throw her about or carry her elsewhere.

Relations with other beetles and parasites.

Other lucanid species found in the same logs in close proximity to *P. muelleri* include *Lamprima latreillei* W.S. Macleay, *Rhyssonotus nebulosus*

(Kirby), *Prosopocoilus torresensis* (Deyrolle), *Figulus* sp., *Aegus jansoni* Boileau, *Syndesus cornutus* (Fabricius), and *Cacostomus squamosus* Newman. The first three species appear to be white rot associated but tend to utilise different niches. *L. latreillei* prefers drier sites and is more common in dead standing timber than in logs on the ground. *R. nebulosus* tends to be most common in sapwood and *P. torresensis* is less common with increasing elevation. Although they can be found in the same timber as *P. muelleri*, *A. jansoni* and *S. cornutus* are brown rot associated species. Brown rot is the result of fungal attack in which the cellulose has been destroyed leaving the dark coloured lignin. This is evidenced by zones of darker colour in the wood, dark brown to rust-red in colour. Brown rot does not have a "stringy" texture but tends to be powdery. *C. squamosus* is found in detritus in cracks in wood and under logs and is not clearly associated with either type of rot.

Larvae of the cetoniine *Schizorhina atropunctata* (Kirby) are commonly found with white rot-feeding lucanid larvae, feeding on their faeces and fragmented wood. Larvae of another cetoniine, *Lenosoma* sp. also have been found feeding on *P. muelleri* larval frass.

Larvae of *P. muelleri* are parasitised commonly by the fly *Amphibolia ignorata* Paramonov (Tachinidae) (Fig. 9). They are also parasitised by the wasp *Liacos insularis* (Smith) (Scoliidae) (Fig. 9): larvae attach to final-instar *P. muelleri* larvae and pupae (Fig. 10), the egg being laid on the underside, just behind the legs. *L. insularis* was only observed on the edge of rainforest. The beetle *Mordella elongatula* (Macleay) (Mordellidae) (Fig. 9), one specimen of which emerged from a pupal cell of *L. insularis*, is possibly a hyperparasite but this habit is not usual for mordellid beetles.

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